

Compensatory dynamics are rare in natural ecological communities

J. E. Houlahan^{a,b}, D. J. Currie^c, K. Cottenie^d, G. S. Cumming^e, S. K. M. Ernest^f, C. S. Findlay^c, S. D. Fuhlendorf^g, U. Gaedke^h, P. Legendreⁱ, J. J. Magnuson^j, B. H. McArdle^k, E. H. Muldavin^l, D. Noble^m, R. Russellⁿ, R. D. Stevens^o, T. J. Willis^p, I. P. Woiod^q, and S. M. Wondzell^r

^aDepartment of Biology, University of New Brunswick, P.O. Box 5050, Saint John, NB, Canada E2L 4L5; ^bOttawa–Carleton Institute of Biology, University of Ottawa, Ottawa, ON, Canada K1N 6N5; ^cDepartment of Integrative Biology, University of Guelph, Guelph, ON, Canada N1G 2W1; ^dPercy FitzPatrick Institute, University of Cape Town, Rondebosch, Cape Town 7701, South Africa; ^eDepartment of Biology, Utah State University, Logan, UT 84322; ^fDepartment of Plant and Soil Science, Oklahoma State University, 368 AGH, Stillwater, OK 74078; ^gInstitute of Biochemistry and Biology, University of Potsdam, Maulbeerallee 2, D-14469 Potsdam, Germany; ^hDépartement de Sciences Biologiques, Université de Montréal, C.P. 6128, Succursale Centre-ville, Montréal, PQ, Canada H3C 3J7; ⁱCenter for Limnology, University of Wisconsin, Madison, WI 53706; ^jDepartment of Statistics, University of Auckland, Private Bag 92019, Auckland, 1, New Zealand; ^kDepartment of Biology, University of New Mexico, Albuquerque, NM 8731; ^lNational Centre for Ornithology, The Nunnery, British Trust for Ornithology, Thetford, Norfolk IP 24 2PU, United Kingdom; ^mEarth Institute, Columbia University, New York, NY 10025; ⁿDepartment of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803; ^oDepartment of Zoology, University of Toronto, Toronto, ON, Canada M5S 3G5; ^pPlant and Invertebrate Ecology Division, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, United Kingdom; and ^qForest Service, Pacific NW Research Station, Forestry Science Laboratory, U.S. Department of Agriculture, 3625 93rd Avenue, Olympia, WA 98512

Edited by Rodolfo Dirzo, Stanford University, Stanford, CA, and approved December 28, 2006 (received for review May 9, 2006)

In population ecology, there has been a fundamental controversy about the relative importance of competition-driven (density-dependent) population regulation vs. abiotic influences such as temperature and precipitation. The same issue arises at the community level; are population sizes driven primarily by changes in the abundances of cooccurring competitors (i.e., compensatory dynamics), or do most species have a common response to environmental factors? Competitive interactions have had a central place in ecological theory, dating back to Gleason, Volterra, Hutchinson and MacArthur, and, more recently, Hubbell's influential unified neutral theory of biodiversity and biogeography. If competitive interactions are important in driving year-to-year fluctuations in abundance, then changes in the abundance of one species should generally be accompanied by compensatory changes in the abundances of others. Thus, one necessary consequence of strong compensatory forces is that, on average, species within communities will covary negatively. Here we use measures of community covariance to assess the prevalence of negative covariance in 41 natural communities comprising different taxa at a range of spatial scales. We found that species in natural communities tended to covary positively rather than negatively, the opposite of what would be expected if compensatory dynamics were important. These findings suggest that abiotic factors such as temperature and precipitation are more important than competitive interactions in driving year-to-year fluctuations in species abundance within communities.

biological interactions | community dynamics | negative covariance | neutral models | zero-sum

A foundational controversy in ecology has centered on the long-term stability of population and community abundance, sometimes called “the balance of nature” (1). Darwin's famous “struggle for existence” on the “entangled bank” poetically expressed Thomas Malthus' principal idea that species' capacity to reproduce greatly exceeds their resources (2). Hence, fierce competition should structure the species and assemblages we see today. Similarly, papers in the 1920s–1950s presented the view that population abundances fluctuate much less than their intrinsic rates of increase would allow (3–5). This observation suggested to early ecologists that populations were regulated by density-dependent factors, and that competition was the most plausible underlying mechanism. In contrast, other authors emphasized abiotic environmental factors as the primary drivers of population fluctuations, often largely in the absence of competition (6–9). Recurring debates about the relative impor-

tance of biotic regulation vs. abiotic forcing have been dubbed “ecology's 12-year cycle” (1, 10).

The same set of issues applies at the community level. Diamond (11), Tilman (12, 13), and Wisheu and Keddy (14), among others, have presented models of plant community structure based on the relative competitive abilities of community members. More recently, Hubbell's (15) unified neutral theory of biodiversity and biogeography similarly, “. . . rests on a key first principle, namely that the interspecific dynamics of ecological communities is a stochastic zero-sum game” (16). That is, the total number of individuals in a community is constant or at least only stochastically varying.

Yet, Cooper (1) points out that arguments about the balance of nature, “attempt to settle questions about what kinds of ecological factors are most important, as determinants of demographic behavior and/or community structure, from a largely *a priori* perspective, with at best a smattering of empirical cases sprinkled in for good measure.” For example, in Hubbell's book (15), support for the zero-sum assumption comes in the form of: (i) an empirical linear relationship between the size of the sampling unit (SU) and the number of individual trees found on a 50-hectare plot on Barro Colorado Island, Panama; and (ii) logical arguments based on finite resources. The empirical relationship is unconvincing because, whereas a positive area–abundance relationship is necessary in a world where biological communities are saturated, it is certainly not sufficient. Hubbell's (15) logical arguments about communities resemble Lack's arguments about individual populations: “Limiting resource availability per unit area will ultimately impose a finite limit on the density of competing organisms within a given ecological community in a defined space”. This argument works only if communities are assumed always to be at or near carrying capacity. Hubbell ends this discussion with the statement of a general principle, that “large landscapes are essentially always

Author contributions: J.E.H., D.J.C., K.C., G.S.C., S.K.M.E., C.S.F., S.D.F., U.G., P.L., J.J.M., B.H.M., E.H.M., D.N., R.R., R.D.S., T.J.W., I.P.W., and S.M.W. designed research; J.E.H. performed research; J.E.H. contributed new reagents/analytic tools; J.E.H. and I.P.W. analyzed data; and J.E.H. and D.J.C. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS direct submission.

Abbreviation: SU, sampling unit.

^bTo whom correspondence should be addressed. E-mail: jeffhoul@unbsj.ca.

This article contains supporting information online at www.pnas.org/cgi/content/full/0603798104/DC1.

© 2007 by The National Academy of Sciences of the USA

biotically saturated with individuals" (15). This assertion, in our view, is an open empirical question.

Operationally, theories that postulate strong competitive interactions (such as centrifugal organization and resource partitioning) and neutral model zero-sum community dynamics both imply that communities will show compensatory dynamics. This hypothesis makes a strong prediction. By the strictest definition, it predicts that (as Hubbell states; ref. 15), "any increase in one species must be accompanied by a matching decrease in the collective number of all other species in the community". A less-stringent definition that allows for limited stochastic variation implies that the covariance among population abundances in a community must, on average, be negative.

To test for negative covariance among species, we calculated a community-level measure of covariance (i.e., the sum of all pair-wise covariances). The variance of a sum can be expressed as the sum of all possible variances and covariances (17), providing an analytical tool for detecting compensatory dynamics within communities (17–19). That is, the variance of community abundance can be expressed as the sum of all of the species variances plus all of the pair-wise species covariances. For example, in a two-species community comprising species x and y , $\sigma^2(x + y) = \sigma^2(x) + \sigma^2(y) + 2\sigma(x, y)$, where $\sigma^2(x)$ = the temporal variance in abundance of species x , $\sigma^2(y)$ = the temporal variance in abundance of species y , $\sigma(x, y)$ = the temporal covariance in abundance of species x and y , and $\sigma^2(x + y)$ = the temporal variance in the combined abundance of species x and y . More generally, in an n species community, $\sigma^2(\sum_{i=1}^n x_i) = \sum_{i=1}^n \sigma^2(x_i) + 2 \sum_{i < j} \sigma^2(x_i, x_j)$. Thus, we can compute the total covariance for a community as $\sum_{i=1}^n \sum_{j < i} \sigma^2(x_j, x_i) = (\sigma^2(\sum_{i=1}^n x_i) - \sum_{i=1}^n \sigma^2(x_i))/2$. In a community with zero-sum dynamics, the variance of the sum is zero. Because the sum of the variances is a positive number, these simple equations show that the sum of the covariances must be negative. We used this method to calculate community covariance for each of the communities in each of 41 data sets (Table 1).

Results and Discussion

We estimated the distribution of community covariances in different SU for 41 different plant and animal data sets; 36 of 41 data sets showed >50% positive covariances (Fig. 1). Thirty-one of those had more positive covariances than would be expected by chance alone (assuming zero covariance). Only 3 of 41 data sets had fewer positive covariances than would be expected by chance ($\alpha = 0.10$), all of which were plant communities: trees from the Hubbard Brook Bird Area plots at the quadrat scale (25 × 10 m), Cedar Creek plants at the transect scale, and Sonoran herbaceous plants at the line scale. Indeed, even the tree community on Barro Colorado Island (BCI) on which Hubbell based his theoretical concepts showed strong positive covariance over six sampling periods from 1981 to 2005 (mean = 232,868; coefficient of variation = 0.052; covariance = 124,105,931) (note: the BCI data are not part of the 41 data sets analyzed here, because we used only data sets that had multiple sites). Our results demonstrate that positive covariance among species is far more common in nature than negative covariance (Fig. 1).

However, the distribution of community covariances is scale-dependent. Nine data sets analyzed here have data for at least two spatial scales and, in eight of nine cases, the smaller spatial scales have an equal or larger proportion of negative covariances (although still <50% in most cases) (Fig. 2), which implies that the factors causing negative covariance between species may be more important at small than large scales.

Why did we observe so few negatively covarying species dynamics? Hubbell (15) suggested three cases in which the zero-sum assumption might not hold: (i) aggregation of taxa that are not at the same trophic level, (ii) a severe disturbance regime

that maintains community abundance at levels below carrying capacity, and (iii) spatial variability in productivity (1). We have constrained our analyses to communities of species of similar trophic status, so inappropriate aggregation is unlikely to be the explanation for the ubiquity of positive covariances. In addition, for two of the data sets (i.e., Rothamsted moths and Wisconsin Lake fish), we were able to analyze subsets of the communities likely to have more similar resource requirements (e.g., planktivorous fish rather than all fish). We would expect that more trophically similar communities would show more negative covariances than less trophically similar communities if a lack of trophic similarity was a cause of the positive covariances, but we found little evidence that this prediction was true (Rothamsted moths, all moths had 105 sites with positive covariance and 0 with negative covariance; Noctuid moths, 105:0; Geometrid moths, 103:2; Ennominaea moths, 95:8; Wisconsin fish, all fish 3:2; zooplanktivores, 3:2; benthivores, 4:1; and piscivores, 2:3).

The second and third explanations are both subsets of a more general possibility consistent with our results, i.e., that the abundances of large sets of species in a community vary in response to a common set of environmental drivers. It would not be surprising that many coexisting species respond similarly to disturbance, temporal variability in productivity, and fluctuations in climatic conditions. Fischer *et al.* (20), for example, showed that compensatory dynamics are limited in communities where species respond in similar ways to changing environmental conditions. Synchronized fluctuations in abundance over time would be reflected in generally positive covariance among abundances of species in communities. Positive covariance suggests that the proposition that "large landscapes are essentially always biotically saturated with individuals" (15) is not true, or at least that the carrying capacity for large landscapes varies dramatically over time, primarily in response to environmental drivers (21).

More broadly, our results show that competition is unlikely to be the primary factor responsible for observed variability in community abundance over time. This does not preclude pair-wise negative covariances between individual pairs of species, nor does it rule out differing competitive responses to the primary factors that drive community abundance. Rather, our results suggest that the signature of competition on temporal variability in community abundance is weak compared with the signature of other, probably abiotic, forcing variables.

The results, from many natural communities and across multiple scales, suggest that community-level negative covariance in abundance is generally rare. Our results have important implications for ecological hypotheses that emphasize competition as the primary driver of community dynamics, such as centrifugal (14) and resource partitioning (13) theories, because our results suggest that the primary driver of community dynamics is abiotic environmental forcing, not competition. Our results do not rule out the possibility of "ghosts of competition past" (22, 23), i.e., communities structured to minimize competition, but they strongly suggest that fluctuations in abundance are not driven primarily by competition. An additional caveat is that we have examined communities over relatively short temporal scales. It may be that disturbance events and environmental variability drive community dynamics over short time periods, whereas over longer time periods, competition would lead to more negative covariances.

Similarly, our results also impact the unified neutral theory of biodiversity and biogeography (15). Its assumption of zero-sum community dynamics is apparently not commonly found in nature. That said, neutral model theory and our analyses have focused on the abundance of organisms, but there is theoretical and empirical evidence suggesting that compensatory dynamics are more likely to be seen in variables such as biomass and energy utilization than in abundance (18, 24, 25). It is possible that

Table 1. Data sets used in covariance analyses

Data set	Abbreviation	Taxa	Sampling period	Time interval, yr (times sampled)	Scale	Sampling units
						(mean CV of community abundance)
Harvard Forest, Massachusetts, Lyford Mapped Tree Plot	HLF	Trees	1969–2001	5–17 (4)	920 m ²	32 (0.212)
Harvard Hurricane Recovery Plot	HHRP	Trees	1937–1991	3–30 (5)	250–1,000 m ²	14 (0.132)
Harvard Pisgah Forest Plots	HPF	Trees	1984–2001	5–6 (4)	400 m ²	14 (0.909)
Hubbard Brook, New Hampshire, Bird Area	HBBAQ	Trees	1991–2003	2 (7)	250 m ²	234 (0.067)
	HBBAAT	Trees	1991–2003	2 (7)	10,000 m ²	4 (0.010)
Hubbard Brook, New Hampshire, Watershed 6	HBW6	Trees	1965–2002	5–12 (7)	625 m ²	208 (0.362)
Sonora	SPL	Herbs	1949–1992	1–14 (21)	0.09 m ²	288 (0.777)
	SPP	Herbs	1949–1992	1–14 (21)	1,200-m transect	24 (0.602)
	SPPa	Herbs	1949–1992	1–14 (21)	Pasture (various sizes)	8 (0.523)
Portal, New Mexico	PWAS	Winter annuals	1989–2002	1 (14)	0.25 m ²	384 (1.782)
	PWAP	Winter annuals	1989–2002	1 (14)	2,500 m ²	24 (1.226)
	PSAS	Summer annuals	1989–2002	1 (14)	0.25 m ²	384 (1.715)
	PSAP	Summer annuals	1989–2002	1 (14)	2,500 m ²	24 (1.839)
Big Bend, Texas	BBPT	All plants	1955–1996	6–15 (5)	1.85 m ²	51 (1.049)
	BBPS	All plants	1955–1996	6–15 (5)	5.5 m ²	17 (1.118)
	BBPeT	Perennials	1955–1996	6–15 (5)	1.85 m ²	51 (1.054)
	BBPeS	Perennials	1955–1996	6–15 (5)	5.5 m ²	17 (1.123)
Cedar Creek, Minnesota	CCF	All plants	1988–1998	1 (11)	Field (various sizes)	14 (0.367)
	CCT	All plants	1988–1998	1 (11)	12 m ²	52 (0.438)
Jornada, New Mexico	JPQ	All plants	1989–2002	1 (14)	1 m ²	734 (0.524)
	JPS	All plants	1989–2002	1 (14)	6,400 m ²	15 (0.380)
	JPZ	All plants	1989–2002	1 (14)	Vegetation zones (various sizes)	5 (0.339)
Rothamsted, United Kingdom	RM	Moths	1965–2003	1 (10–39)	Light-trap	105 (1.264)
	RE	Ennominids	1965–2003	1 (10–39)	Light-trap	103 (0.460)
	RG	Geometrids	1965–2003	1 (10–39)	Light-trap	105 (0.403)
	RN	Noctuids	1965–2003	1 (10–39)	Light-trap	105 (0.406)
Wisconsin LTER Lakes	WF	Fish (all trophic levels)	1981–2001	1 (21)	Whole-lake	5 (1.015)
	WB	Benthivore fish	1981–2001	1 (21)	Whole-lake	5 (0.883)
	WP	Piscivore fish	1981–2001	1 (21)	Whole-lake	5 (0.553)
	WZ	Zooplanktivore fish	1981–2001	1 (21)	Whole-lake	5 (1.269)
Konza LTER, Kansas	KMSL	Small mammals (spring)	1982–1997	1 (16)	300-m trapline (20 traps)	14 (0.917)
	KMSW	Small mammals (spring)	1982–1997	1 (16)	Watershed	7 (0.840)
	KMAL	Small mammals (autumn)	1982–1997	1 (16)	300-m trapline (20 traps)	12 (0.714)
	KMAW	Small mammals (autumn)	1982–1997	1 (16)	Watershed	6 (0.663)
Konza LTER, Kansas	KG	Grasshoppers	1982–1991 and 1996–2003	1 (7–19)	Watershed	10 (1.250)
Sevilleta, New Mexico	SSpR	Rodents (spring)	1989–2003	1 (15)	444 trap grid	6 (0.798)
	SSR	Rodents (summer)	1989–2003	1 (15)	444 trap grid	6 (0.777)
United Kingdom Butterfly Monitoring Scheme	BMS	Butterflies	1976–2002	1 (10–27)	2,000–4,000 m	58 (0.539)
Cedar Creek, Minnesota	CCG	Grasshoppers	1989–1998	1 (10)	Field (various sizes)	20 (0.697)
Jornada, New Mexico	JM	Small mammals	1989–1994	1 (6)	1,000-m transect	5 (1.362)
Jornada, New Mexico	JR	Reptiles	1989–1994	1 (6)	1,000-m transect	5 (0.721)

ILTER, National Science Foundation Long-Term Ecological Research; CV, coefficient of variation.

zero-sum assumptions about biomass and energy use may be more consistent with patterns seen in nature than zero-sum abundance assumptions.

The neutral model of molecular evolution has demonstrated that neutral theories can avoid the zero-sum assumption (26), but it has done so by incorporating the concept of “effective population size”

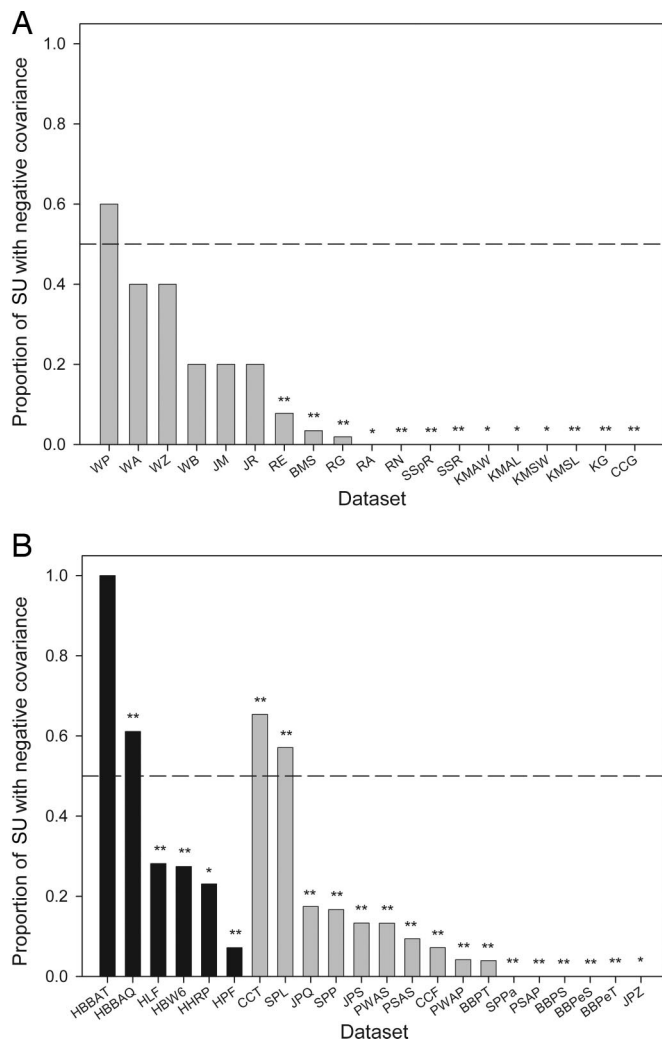


Fig. 1. The proportion of SU communities in multicommunity data sets that had community-level negative covariances (**, $P < 0.05$; *, $P < 0.10$; P values were obtained from median tests; H_0 , median covariance = 0). (A) Animal communities. (B) Tree (black bars) and herbaceous plant (gray bars) communities.

(27); it may be that ecological neutral models require an analogous concept of effective community size. Currently, most ecological neutral models assume that communities are zero-sum, although He (28) has developed neutral models that do not incorporate the restrictive zero-sum assumption, an important step in the evolution of ecological neutral model theory.

Hubbell's model (15) further assumes that species are functionally equivalent. The positive covariances among species that we find in most communities are consistent with this idea, because functionally equivalent species would be expected to respond similarly to their environment. Thus, despite demonstrating that the zero-sum assumption is not common in nature, our results remain consistent with one obvious assumption of neutral theory.

In conclusion, our results suggest that variability in community abundance appears to be driven more by processes that cause positive covariation among species (e.g., similar responses to the environment) than processes that cause negative covariation among species (e.g., the direct effects of competition for scarce resources).

Data and Methods

We estimated the distribution of community covariances for 41 different multicommodity plant and animal data sets that were

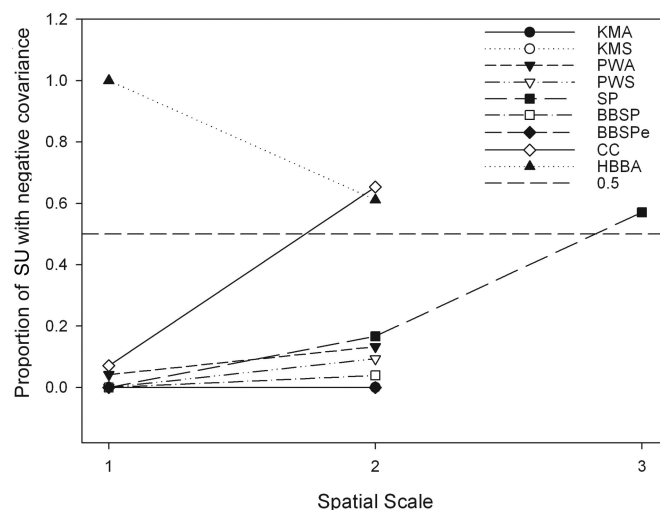


Fig. 2. The relationship between the proportion SU of communities with negative covariance and spatial scale for all multicommunity data sets that were sampled at multiple scales. The abscissa is the rank of spatial grain size for a particular data set from largest to smallest (i.e., there is no absolute spatial scale associated with the values along the abscissa. Sonoran plants (SP); Portal summer annuals (PSA); Portal winter annuals (PWA); Big Bend plants, all species (BBSP); Big Bend plants, perennial species (BBSPe); Hubbard Brook Bird Area trees (HBBA); Cedar Creek plants (CC); Jornada plants (JP); Konza summer mammals (KMS); and Konza autumn mammals (KMA).

either contributed by coauthors and/or are publicly available (Table 1). We constrained our analyses to data sets that included only organisms from the same trophic level, because zero-sum hypotheses hold only for organisms on the same trophic level. More generally, species in different trophic levels are much less likely to compete than species on the same level. Each of these data sets was comprised of multiple sites (SU) with the communities sampled over multiple years [Table 1; see supporting information (SI) *Appendix 1* for a more detailed description of the data sets used]. In some cases, site data were collected at different spatial scale and for different taxonomic subsets of the total data set. We separately analyzed data collected at different spatial scale and for different taxonomic subsets. For example, plant data from Portal, AZ, were collected at two spatial scales: the $50 \times 500\text{-m}$ plot scale and 0.25-m^2 scale and for two life history guilds, summer and winter annuals. Thus, we analyzed four different subsets of the Portal data set: summer annuals at plot and quadrat scales and winter annuals at plot and quadrat scales (Table 1). The resulting lack of independence among some data sets is not relevant because we did not conduct statistical analyses across data sets.

We estimated the distribution of community covariances in the different SU for each of the 41 data sets and used a two-tailed binomial test to ascertain whether the median value for each data set was significantly different from zero (29) (e.g., the plant data set from Portal at the plot scale has 24 sites; all 24 sites showed positive community covariance, and we did a two-tailed binomial test that showed that the median value of the community covariances for those 24 sites was significantly different from zero). Negative community covariances indicate that a decline in one species is compensated by an increase in other species, whereas positive community covariances imply that species increase or decline together.

We thank all of the researchers and scientists who generously make their data publicly available. In addition, we thank the National Center for Ecological Analysis and Synthesis for funding the research and hosting our meetings.

1. Cooper GJ (2003) *The Science of the Struggle for Existence* (Cambridge Univ Press, Cambridge, UK).
2. Darwin C (1981) *On the Origin of Species: A Facsimile of the First Edition* (Harvard Univ Press, Cambridge, MA).
3. Elton C, Nicholson M (1942) *J Anim Ecol* 11:215–244.
4. Nicholson AJ (1933) *J Anim Ecol* 2:131–178.
5. Lack D (1954) *The Natural Regulation of Animal Numbers* (Clarendon, Oxford).
6. Andrewartha HG, Birch LC (1954) *The Distribution and Abundance of Animals* (University of Chicago Press, Chicago).
7. den Boer PJ, Reddingius J (1996) *Regulation and Stabilization. Paradigms in Population Ecology* (Chapman & Hall, London).
8. Strong DR, Jr (1983) *Am Nat* 122:636–660.
9. White TCR (2001) *Oikos* 93:148–152.
10. May RM (1984) in *Ecological Communities: Conceptual Issues and the Evidence*, eds Strong DR, Simberloff D, Abele LG, Thistle AB (Princeton Univ Press, Princeton, NJ), pp 3–18.
11. Diamond JM (1975) in *Ecology and Evolution of Communities*, eds Cody ML, Diamond JM (Belknap, Cambridge, MA), pp 342–444.
12. Tilman D (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities* (Princeton Univ Press, Princeton, NJ).
13. Tilman D (1985) *Am Nat* 125:827–852.
14. Wisheu IC, Keddy PA (1992) *J Veg Sci* 3:147–156.
15. Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton Univ Press, Princeton, NJ).
16. Hubbell SP (1997) *Coral Reefs* 16:S9–S21.
17. Schluter D (1984) *Ecology* 65:998–1005.
18. Ernest SKM, Brown JH (2001) *Ecology* 82:2118–2132.
19. Frost TM, Carpenter SR, Ives AR, Kratz TK (1995) in *Linking Species and Ecosystems*, eds Jones CG, Lawton JH (Chapman & Hall, New York), pp 224–239.
20. Fischer JM, Frost TM, Ives AR (2000) *Ecol Appl* 11:1060–1072.
21. del Monte-Luna P, Brook BW, Zetina-Rejon MJ, Cruz-Escalona VH (2004) *Glob Ecol Biogeog* 13:485–495.
22. Pritchard JR, Schluter D (2001) *Evol Ecol Res* 3:209–220.
23. Rosenzweig ML (1981) *Ecology* 62:327–335.
24. Chapin FS III, Shaver GR (1985) *Ecology* 66:564–576.
25. Wardle DA, Bonner KI, Barker GM, Yeates GW, Nicholson KS, Bardgett RD, Watson RN, Ghani A (1999) *Ecol Mono* 69:535–568.
26. Kimura M (1983) *The Neutral Theory of Molecular Evolution* (Cambridge Univ Press, Cambridge, UK).
27. Crow JF, Kimura M (1970) *An Introduction to Population Genetics* (Harper & Row, New York).
28. He F (2005) *Funct Ecol* 19:187–193.
29. Zar JH (1996) *Biostatistical Analysis* (Prentice-Hall, Upper Saddle River, NJ).